

A New Species of *Ibalia* from Borneo, with a Revised Phylogeny and Historical Biogeography of Ibaliiidae (Hymenoptera: Cynipoidea)¹

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Abstract.—*Ibalia kalimantanica* Liu from eastern Kalimantan, Borneo, is described here as a new species. Reanalysis of a previously published character matrix of the family Ibaliiidae with the new species included shows that *I. kalimantanica* belongs to the subgenus *Tremibalia* and is the sister species to the clade of (*I. mirabilis*, *I. japonica*), *I. humanica*). Biogeographical analysis of the expanded data set strengthened support for an earlier hypothesis concerning the historical biogeography of the Ibaliiidae postulating early radiation of the family in the eastern Palaearctic—Oriental region. The separation of the *I. kalimantanica* clade is suggested to have been caused by changes of land area configuration in Southeast Asia as a result of global sea level changes during late Oligocene to early Miocene.

The Ibaliiidae constitute a small family of parasitic cynipoids comprising nineteen known species, of which all but one are restricted in the Northern Hemisphere. The species belong to the three genera *Eileenella* Fergusson, *Heteribalia* Sakagami and *Ibalia* Latreille. They parasitize siricid woodwasps, both in conifers and hardwoods, and some species of *Ibalia* have been used in the biological control of siricid pests in conifer plantations. Ibaliiidae is of interest owing to its near-basal phylogenetic position within the superfamily Cynipoidea (Ronquist 1995). Recently, Liu & Nordlander (1992, 1994) studied the North-American species of the Ibaliiidae and presented a review of the world species of the family, and Nordlander et al. (1996) studied their phylogeny and historical biogeography. In this study, a new species of *Ibalia* Latreille is described from

the tropical rain forests of eastern Kalimantan, Borneo, Indonesia. The character matrix of Nordlander et al. (1996) has been reanalyzed in order to determine the phylogenetic position of the new species in relation to other *Ibalia* species, and to investigate whether the topology of the phylogenetic tree of the genus would be thus affected.

Species of *Ibalia* have previously been described only from the Northern Hemisphere; the new species represents the first tropical species of the genus. The only other tropical ibaliid species, *Eileenella catherinae*, is from New Guinea, and is the sister species to all other ibaliids (Fig. 2). Therefore, the phylogenetic position of the new *Ibalia* species will provide new evidence for testing the previous biogeographical scenario of Nordlander et al. (1996).

MATERIALS AND METHODS

Terminology used in this article follows that of Ronquist and Nordlander (1989) and Liu and Nordlander (1994).

Only a single female of the new species was available. The character-state coding of the new species was made in compari-

¹ This paper appeared in *Acta Universitatis Suevicæ Silvæstris* 62(1998) but was not intended for permanent scientific record as stated in the Disclaimer published on page 6 of that publication. This Disclaimer satisfies Chapter III, Article 8, section b, of the ICZN. (Editor)

Table 1. Character states for *Ibalia kalimantanica*. Characters and character states are coded as in Nordlander et al. (1996), with the following addition of character state: Character 55. Sculpture of mesopleural speculum: (2) distinctly vertically costate with secondary irregular foveolate sculpture. The table is supplementary to the previously published matrix including all the other species.

Taxon	Character							
	1	6	11	16	21	26	31	36
<i>I. kalimantanica</i>	11???	11100	10100	01-00	0-011	00-10	00120	010-1

son with representatives of the genus *Heteribalia* Sakagami and each of the two subgenera of *Ibalia*, as well as of the outgroups Liopteridae and *Eileenella* Ferguson.

The characters and character coding were the same as in the previous cladistic analysis of the Ibalidae (Nordlander et al. 1996). For characters 31, 34, 35, and 69, a polymorphic condition was coded as a separate, intermediate state and each step was given the weight 0.5, so that a change between non-polymorphic states would count as one step instead of two. Of the multi-state characters, characters 6, 45, 52, 63, 66, 67, and 80 were unordered; the others were ordered in the sequence 012. The only change in relation to the previous study was that an autapomorphy for *I. kalimantanica* required additional state for character 55 (see Table 1).

Methods used for phylogenetic and biogeographical analyses were in general as described in Nordlander et al. (1996), with some minor modifications. As in Nordlander et al. (1996), PAUP 3.1 were used for

phylogenetic analysis, but less extensive options were adopted when calculating support indexes for the branches. Options for bootstrapping included heuristic search, random addition sequence, 1000 replications, and for each replication tree search options are simple addition sequence and tree bisection reconnection (TBR) swapping. The decay index (or Bremer support), the number of extra steps needed to break up the group, were obtained using branch and bound search and simple addition sequence. For biogeographical analysis, the previously defined distribution area Eastern Palearctic + North-east Oriental was extended to include oceanic Southeast Asia, and defined as Eastern Palearctic + Eastern Oriental. DIVA1.1 was used in the present study for historical reconstruction (Ronquist 1996, 1997). It is basically the same as the earlier version (DIVA 1.0) used by Nordlander et al. (1996), but with some performance improvements (Ronquist 1996) that should not affect comparison of the results.

Ibalia (Tremibalia) kalimantanica Liu,
new species
(Fig. 1)

Female.—Body length 10.0 mm. *Coloration*: Head yellow except eyes, upper face, and a narrow longitudinal median strip through lower face, which are black. Flagellomeres 4–10 of female antenna white to pale, contrasting with the remaining darker antennal segments. Pronotum pale yellow with anterior plate of pronotum medially, dorsal pronotal area entirely, and lateral pronotal area posteriorly black.



Fig. 1. *Ibalia kalimantanica*, new species.

Table 1. Extended.

41	46	51	56	61	66	71	76	81
0-012	01111	00102	10100	0-011	11001	?100?	-----	--

Mesothorax mainly black, a small area posteriorly on mesoscutum, mesopleural triangle entirely, and a broad transverse band across middle of scutellum yellow. Metathorax and propodeum black. Legs

yellow with dorsal parts of coxa, trochanter, and femur yellow to brown. Metasoma pale yellow with three narrow, transverse to oblique, dark brown strips (Fig 1).
Head.—Vertex rather weakly longitudi-

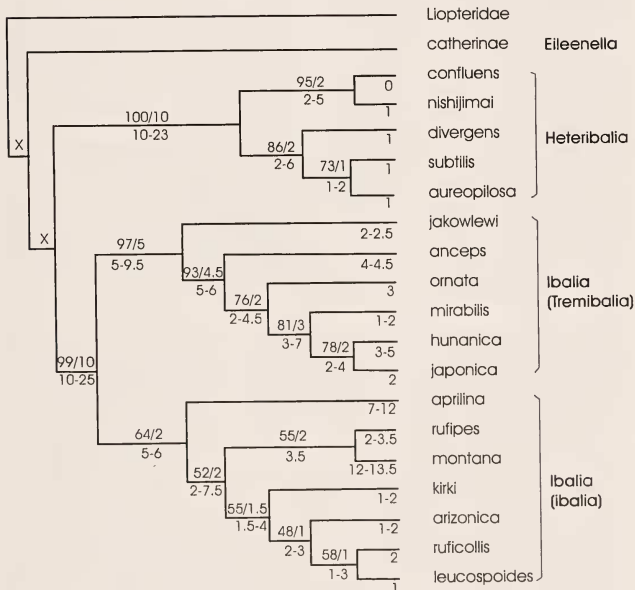


Fig. 2. Shortest tree of interspecific relationships in the Ibalidae according to the previous analysis by Nordlander et al. (1996). Figures above and below branches as in Fig. 3.

nally carinate and with rather dense, adpressed pubescence. Upper face completely rugose; antennal scrobes indistinctly delimited by a lateral carina and not distinctly depressed. Gena largely glabrate with shallow foveae, postero-ventrally distinctly costate. Eye length about 3.1 times length of malar space.

Antenna.—Female with 11 flagellomeres; 2nd flagellomere distinctly longer than 1st ($F2/F1 = 4/3$).

Mesosoma.—Pronotal crest without medial incision. Pronotum costate almost entirely, covered with dense, adpressed pubescence. Propleuron protruding strongly ventrally. Scutellar foveae rugose, separated by median carina. Posterior processes of scutellum raised weakly posteriorly. Distance between outer sides of posterior scutellar processes about 0.7 times maximum width of scutellum. Femoral groove of mesopleuron almost smooth with faint longitudinal carination ventrally; speculum vertically striate with secondary irregular foveolate sculpture. Metepisternum with vertical costulae. Anterolateral propodeal process distinct; posterior propodeal process low; lateral propodeal carina not elevated medially.

Wings.—Forewing subhyaline with wide dark strip along outer margin and distinct, narrow, dark band between

Rs+M and Cu1 (behind submarginal cell) along outer side of M. Areolet present and very small. Hindwing faintly fuscous along outer margin; with three hamuli.

Legs.—Anterior lateral crest of metacoxa rounded and low. Anterior mesotibial spur present. Anterior apical process of 2nd metatarsomere reaching to middle of 4th tarsomere.

Metasoma.—Metasoma as long as head and mesosoma combined. Tergum 8 with sparse hairs.

Male.—Unknown.

Biology.—Unknown.

Distribution.—Indonesia: E. Kalimantan, Borneo.

Type material.—Holotype, ♀, INDONESIA: Eastern Kalimantan, Kayan-Mentarang Natural Reserve, WWF Station, Lowland Dipterocarpus Forest (2°52'N, 115°49'E), Malaise Trap head, iii.1993 (D.C. Darling and U. Rosichon) (Museum Zoologi Bogor, Indonesia).

For a comprehensive comparison with other species of the family Ibaliiidae, the character matrix of Nordlander et al. (1996) should be consulted. For identification, *I. kalimantanica* may be keyed out by introducing an additional couplet 3a following the second item of couplet 2 in Liu & Nordlander's (1994) key to the world species of *Ibalia*:

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- 3a. Female antenna contrastingly colored with flagellomeres 4–10 white and the remaining segments dark. Upper face lacks regular sculpture. Speculum vertically striate. Posterior processes of scutellum posteriorly only weakly raised . . . *I. kalimantanica* Liu, new species
- Female antenna evenly light yellow to dark brown throughout or becoming darker toward apex, but never with contrasting colors. Upper face longitudinally or transversely carinate at least in antennal scrobes. Speculum finely striolate longitudinally. Posterior processes of scutellum raised distinctly posteriorly 3
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REVISED PHYLOGENY AND HISTORICAL BIOGEOGRAPHY OF IBALIIDAE

The sum of minimum and maximum possible lengths over all characters in the data matrix of Nordlander et al. (1996, Ta-

ble 1) with the data of *I. kalimantanica* added (Table 1) was 99 and 414 respectively. Parsimony analysis using the branch-and-bound algorithm of PAUP resulted in one optimal tree of length 149 (CI = 0.67, RI = 0.84). Compared with Nordlander et

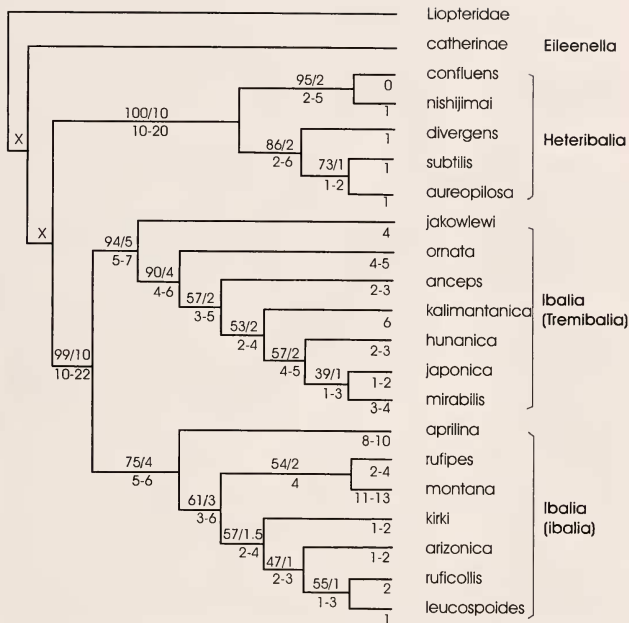


Fig. 3. Shortest tree of interspecific relationships in the Ibalidae, obtained with the branch-and-bound algorithm of PAUP (length = 149, CI = 0.67, RI = 0.84). Shown above each branch in the tree is the support for the corresponding clade, measured as the percentage with which the clade appeared among the shortest trees in 1000 bootstrap replications of the analysis, followed by the decay index (or Bremer support). Below each branch are the minimum and maximum number of character changes along that branch. Clades marked 'x' were constrained to be monophyletic according to results of Ronquist (1995).

al.'s previous optimal tree (length = 141, CI = 0.67, RI = 0.85), the new tree is almost identical in terms of fitness. Compared with the earlier phylogeny of Ibalidae (Fig. 2) as presented by Nordlander et al. (1996), the topology of the phylogenetic tree remained unchanged with the addition of *I. kalimantanica*, except for two local changes within the *Tremibalia* clade.

The first change concerns the relative relationship within the clade (*I. mirabilis* Yasumatsu, *I. japonica* Matsumura, *I. hunanica* Liu & Nordlander), and the other concerns the relative positions of *I. anceps* Say and *I. ornata* Belizin (Figs. 3, 4). The monophyly of *Ibalia* (*Ibalia*) became better supported after the inclusion of *I. kalimantanica* in the analysis, the bootstrap value

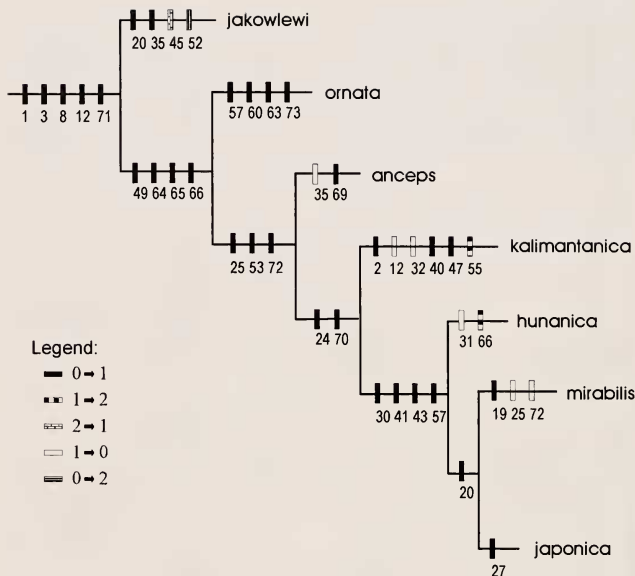


Fig. 4. The clade of *Ibalia* (*Tremibalia*) of the shortest tree with all character changes that could be mapped unambiguously.

increased from 64% to 72% and Bremer support from 2 to 4.

As a result of the changes in tree topology, the previously suggested Eocene-Oligocene separation of *I. anceps* (ca 33–34 MYA) in the subgenus *Tremibalia* is now one node further from the base of the tree (Nordlander et al. 1996). The origin of the Ibaliiidae, based on node/branch distance calculation, is now estimated to be about 160 MYA, a negligible difference from the previous estimate of 150 MYA with regard to potential calculation errors. The estimated time for the origin of the Ibaliiidae is still the Late Jurassic.

An exact search of the updated distribution matrix using DIVA 1.1 resulted in one single reconstruction of the distribution history requiring nine dispersals (Fig. 5). The present reconstruction postulates a center of origin for *Heteribalia* and *Ibalia* in the Eastern Palearctic—North Oriental region, and is in complete accordance with that preferred by Nordlander et al. (1996, Fig. 7).

The separation of the *I. kalimantanica* clade probably resulted from a dispersal within the Oriental as early as in the end of Oligocene (29–24 MYA) and its subsequent isolation from its sister clade. The

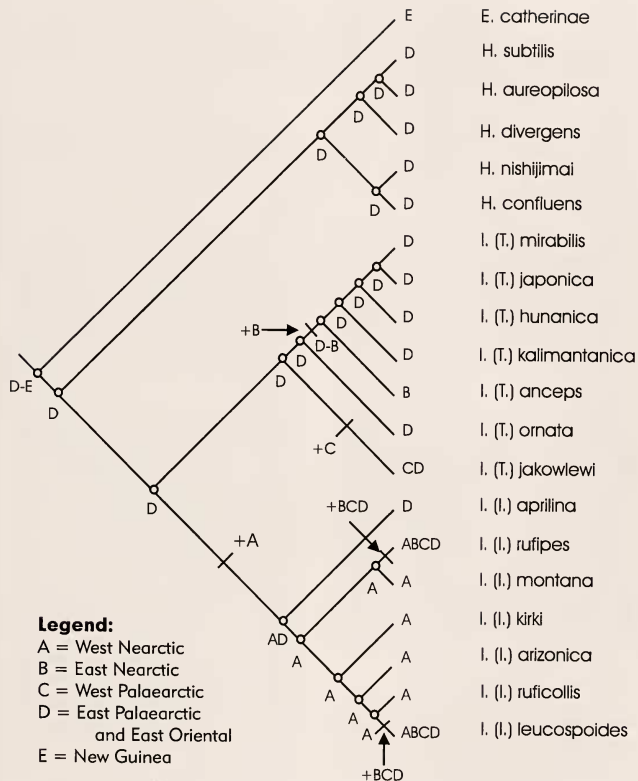


Fig. 5. Reconstruction of ancestral distribution of Ibalidae using DIVA 1.1 resulted in one exact solution that requires nine dispersals. Dispersal events are indicated on the branches, and implied between-area vicariance events are indicated by hyphens in the ancestral distributions.

land area configuration of the Southeast Asia has varied greatly since late Oligocene as a result of global sea level changes (Heaney 1991). The global sea levels re-

mained high from Palaeocene through Oligocene (65–30 MYA). By late Oligocene (29 MYA) there occurred a spectacular fall in sea level to about 250 m below the present-

ent level, and it then recovered to present level by end of Oligocene (24 MYA). From then onwards the sea levels progressively rose, with minor drops, to about 220 m above the present level in the middle Miocene (13 MYA). This was followed by several cycles of fluctuating sea levels (Hutchison 1989). During times of low sea levels, Sumatra, Java and Borneo were part of a peninsula projecting south from continental Asia (often referred to as Sundaland) (Morley & Flenley 1987, Heaney 1991), facilitating the dispersal of the stem species of *I. kalimantanica* and its sister species from the continental Asia to Borneo, and the continuous ancestral distribution was subsequently split when sea level rose again. Although, any of these sea level cycles could have been responsible for the speciation of *I. kalimantanica*, the many autapomorphies of *I. kalimantanica* and the rather many synapomorphies for its sister group indicates that the event probably occurred rather early. Using the same dating method as in Nordlander et al. (1996), the vicariant event separating *I. kalimantanica* from its sister species was estimated as having occurred at about 21 MYA. This is in general accordance with the sea level recovery since late Oligocene from the late Oligocene dramatic drop, which could have facilitated the dispersal of the ancestral species.

ACKNOWLEDGMENTS

I thank Göran Nordlander and Fredrik Ronquist for valuable comments, Chris Darling for presenting me with this pleasant specimen, and Rune Axelsson for photographic assistance. The study was support-

ed by a scholarship from the Oscar and Lili Lamm's Memorial Foundation and by a grant from the Swedish Natural Science Research Council to F. Ronquist and G. Nordlander.

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